Predicting the Ability of Marine Mammal Populations to Compensate for Behavioral Disturbances

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LONG-TERM GOALS

This project has aimed to develop predictive, analytical tools to help determine the ability of marine mammal populations to respond to behavioral disturbances. These tools are to be generic and applicable in a wide range of conditions, including scenarios where data might be limited. Building on recent advances in in the field of behavioral ecology, we have focussed on defining the state resilience of behavioral strategies by considering the transient dynamics of these behavioral strategies, using systems of linear equations. The aim has been to provide a frameworjk that allows an assessment of how probable it is that disturbance events lead to population scale consequences.

OBJECTIVES

- Develop simple, generic measures that allow the estimation of marine mammal populations and individuals to compensate for behavioral disturbances.
- Determining whether behavioral constrainsts can influence this reslience
- Testing these measures against real data from a data rich system
- Use simulations to infer behavioral resilience in data poor conditions

APPROACH

Measure of resilience and predictability exist for a variety of data sets [1]. This project aimed to introduce these measures to the study of animal behavior, using a variety of approaches, including simple theoretical models as well as statistical analysis of data rich conditions. Building on models developed for PCOD [2,3], we aimed to assess resilience of behavioral patterns for individuals in different ecological and life history conditions.

Initially, the approach was to utilise stability analysis of a simple, linear system of ordinary differential equations (ODEs) across a wide range of parameter space for a simple model linking individual's behavior to their condition and the ecological environment they are experiencing. We used some

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simple measures of behavioral resilience that aim to capture both short and long term responses to behavioral disturbance.

Following a detailed analysis of a simple system of ODEs , the approach shifted to analysis of a previously developed model for northern elephant seals (*Mirounga angustirostris*) by Schick et al. [3]. Parameterising this model for multiple individual seals from Año Nuevo in California, and then calculating the resilience measure we developed for each of the individual animals, we can predict which individuals would show the greatest response to disturbance.

Recent studies show that northern elephant seals from Año Nuevo have three different foraging tactics at sea [3]. Some individuals use the Northeast Pacific, while others remain in coastal waters and others again use the North Pacific Transition Zone (NPTZ). Yet, these individuals come from the same colony and therefore have very similar constraints placed on their behavior. Such inter-individual variability can be interpreted as different states of the northern elephant seal's behavior system. Data on these different foraging strategies were derived from an 8-year data set that is composed of measurements of over 300 adult female elephant seals. For these females the Costa Lab at UCSC has measured foraging trip duration, foraging location (i.e. coastal vs NPTZ), mass gain over the trip, body composition over the trip, reproductive parameters (pregnant or not pregnant), and whether the pup survived. Since we have multiple DTAG tracks of the same individual seals across years, we were able to compare individuals across seasons. Considering El Nino climate events as a long term disturbance, we predicted that seals with higher resilience measures would perform better during these long-term climate disturbances when compared to their behavior during a more typical year.

Finally, we have used the same data set to consider shorter term disturbance events. The Costa lab at UCSC's data set also includes dive profiles, from which it is possible to determine activity state (whether the individual is foraging, processing food or transiting through an area of ocean), and dive durations. Previous work by the Costa Lab shows that disturbed dives had a very different profile to others. Assuming activity state dynamics to be Markovian, such that only the current state affects the probability of performing a given action in the near future (timescale of minutes), we can calculate the behavioral transition probabilities for both before and after a disturbance event, and compare those to determine the effects of disturbance events. Resilience measures can be calculated from those transitional probabilities.

WORK COMPLETED

Development of simple, generics measures of behavioral resilience

One way to measure the ability to adapt to disturbance is the concept of resilience. Estimating resilience provides a mean to predict both short- and long-term effects of a disturbance event. Short-term effects are determined by the engineering resilience which describes how long the changes induced by a disturbance event last before the animal returns to its expected behavior. Long-term effects are measured by ecological resilience, or reactivity, which determines how far an individual can be perturbed without falling into an alternative state which may be detrimental, reducing the success of the animal. Mathematically, these resilience measures can be calculated from the Jacobian of a behavioral model, the matrix of partial derivatives for this model. Engineering resilience is given by the maximum absolute value of the real parts of the Jacobian's eigenvalues, $max_i |\ Re(\lambda_i)|$ where λ_i is the i-th eigenvalue of the Jacobian J. Similarly the reactivity of the system is determined by the maximum absolute value of the real parts of the eigenvalues from the matrix $(J + J^T)/2$.

Analysis of a simple model to test predictions from developed measures

We created a simple model linking the feeding behavior F of an individual to both its condition C and the current environment E. We assumed that increased feeding would improve the condition of the individual, while decreasing the environmental quality, and environmental quality will allow an animal to feed more. Increased condition will decrease the individual's propensity to feed, while we include damping on condition such that the condition of an individual will regress towards a mean. Finally, environmental autocorrelation is included, such that a poor environment will remain poor while good quality environments will remain high quality with different scales of autocorrelation (i.e., environmental noise color). These biologically grounded assumptions give the ODE model in Equation 1;

$$\begin{pmatrix} dF/dt \\ dC/dt \\ dE/dt \end{pmatrix} = \begin{pmatrix} -a_1 & -a_2 & a_3 \\ b_1 & -b_2 & 0 \\ -c_1 & 0 & c_3 \end{pmatrix} \quad (1)$$

which gives a single fixed behavioral strategy at the origin, where feeding level, condition and environment measures are all zero. From the Jacobian

$$J = \begin{pmatrix} dF/dF & dF/dC & dF/dE \\ dC/dF & dC/dC & dC/dE \\ dE/dF & dE/dC & dE/dE \end{pmatrix}$$

we can calculate both the stability of the system and the resilience measures introduced above.

Northern elephant seals, and resilience against El Nino climate events

We use the model developed by Schwick et al. [3] to define a system of behavioral equations in which two activities proxys (daily transit rate (T) and daily number of drift dives (V)) are influenced by lipid mass (L) and lipid mass gain is influenced by those two activities:

$$L_t = L_{t-1} + \alpha_0 - \alpha_1 T_t + \alpha_2 V_t - \alpha_3 \frac{L_{t-1}}{R_{t-1}}$$

$$T_t = \beta_0 + \beta_1 \frac{L_t}{R_t} - \beta_2 V_t$$

$$V_t = \gamma_0 - \gamma_1 \frac{L_t}{R_t} - \gamma_2 T_t$$

where $\frac{L_t}{R_t}$ is the lipid to lean mass ratio on day t and R_t is estimated as linearly increasing between two observed measures of R: R_0, lean mass when leaving the colony and R_T, lean mass when returning to the colony[7]. Hence, $\frac{dR}{dt} = r$ a constant daily increased that is estimated from observations.

The Jacobian of this system is

$$J = \begin{bmatrix} 1 - \frac{\alpha_3}{r} & -\alpha_1 & \alpha_2 \\ \frac{\beta_1}{r} & 0 & -\beta_2 \\ \frac{-\gamma_1}{r} & -\gamma_2 & 0 \end{bmatrix}$$

Since the time series of daily lipid mass gain were previously estimated from observations [3] we can therefore fit the system of equations described above to the data (daily lipid mass gain, daily transit rate, and daily number of drift dives) using linear models to estimate the eight parameters in J in order to estimate the stability and resilience of each behavioral strategies. Statistical model fitting allows us to parameterise the model for individual seals for which we have tracks during both an El Nino year and an typical climate year. This allows the calculation of resilience measures from the typical climate year tracks, and comparison of the tracks from El Nino years to those individual's performance in a more typical year.

Shorter term disturbance events

Each individual seal track can be broken down into different dive types for the entire duration of a 7-8 month foraging trip. These 4 types are foraging dives, drift dives (where seals process their food), benthic dives (where seals travel along the sea floor) and 'other', which has previously been assumed to be transit through an area. From studying the dive profiles of confirmed shipping noise events, we determined that dives longer than 5000 seconds were likely to be disturbed dives, where passing ships cause an individual seal to abort dive behavior and sit at depth until the noise created by shipping has dispersed. For the 21 individuals with dives over 5000 seconds, we used continuous time Markov chain techniques to calculate transition intensity matrices for behavior both before and after disturbance events. From the behavior prior to disturbance, resilience measures can be calculated.

RESULTS

Analysis of a simple model to test predictions from developed measures

The equilibrium at the origin for the simple ODE model can be attracting, respulsive of a saddle point where trajectories approach the equilibrium along one or two axes, while being repelled along the remaining axes. Attracting equilibria are more likely to occur when the environmental noise is close to white [4] (lower value for the parameter c_3). Repelling equilibria are more likely when condition is less damped, so the condition of an individual can change quickly (lower value of b_2). Saddles show both high autocorrelation of the environment and condition damping (Figure 1a).

Engineering resilience, or return rate, is higher for stable equilibria than the unstable behavioral systems, but this measure is not higher for stable systems than those that give saddle equilibria (Figure 1b). Reactivity does not significantly differ across stability types, possibly because this simple model only contains a single fixed point. When comparing different stable systems, those with higher engineering resilience show faster return times to the equilibrium than systems with slower predicted return rates (Figure 1c,d).

Northern elephant seals, and resilience against El Nino climate events

From preliminary data, we suggest that ecological resilience, or reactivity, is strongly indicative of success in an El Nino year, with individuals for whom we predict high reactivity showing similar performance in typical and El Nino years, while individuals with lower reactivity gain significantly less weight during an El Nino year (Figure 2).

Shorter term disturbance events

Analysis of the transition intensity matrices of 2 focal individuals shows that behavior changes significantly for seals post disturbance events. Resilience measures for each disturbed individual have also been calculated. This project will terminate on December 1 2014, and during the remaining time, work is focused on developing independent measures of return time to test whether out developed resilience measures actually portray behavior in the Markovian system considered here, as well as extending detailed analysis from the 2 focal individuals considered thus far to all disturbed individuals.

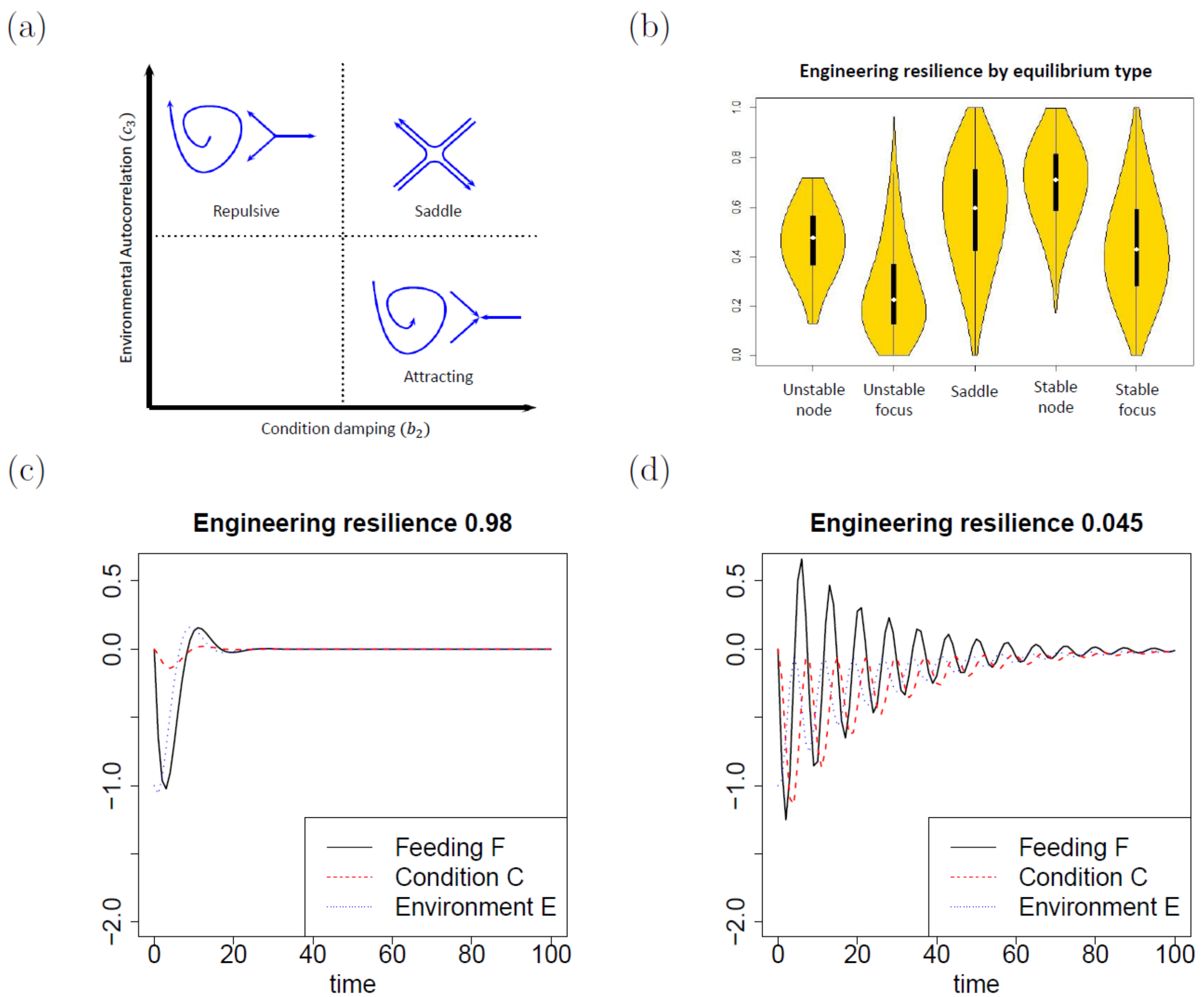

Figure 1: How resilience can predict effects of disturbance.
(a) Stable behavioral systems are more likely to occur when the environment is less correlated in time, such as a white noise environment, while saddles and repulsive systems tend to occur in red or brown noise environments (higher environmental autocorrelation). However, if damping on the individual's condition is reduced, repulsive equilibria are more common. (b) The engineering resilience, or recovery time, for the model in Equation 1, grouped by equilibrium type. The (gold) shading gives the density function for the resilience, while the white dot shows the mean and the thick, black lines show the 50% confidence intervals, while the narrower lines are the 95% confidence intervals. (c-d) Model time series for systems with similar stability (stable foci) but different resilience values when the system is perturbed by decreasing the quality of the environment from the equilibrium value of 0 to -1. The system with the higher engineering resilience showed a faster return to the equilibrium.

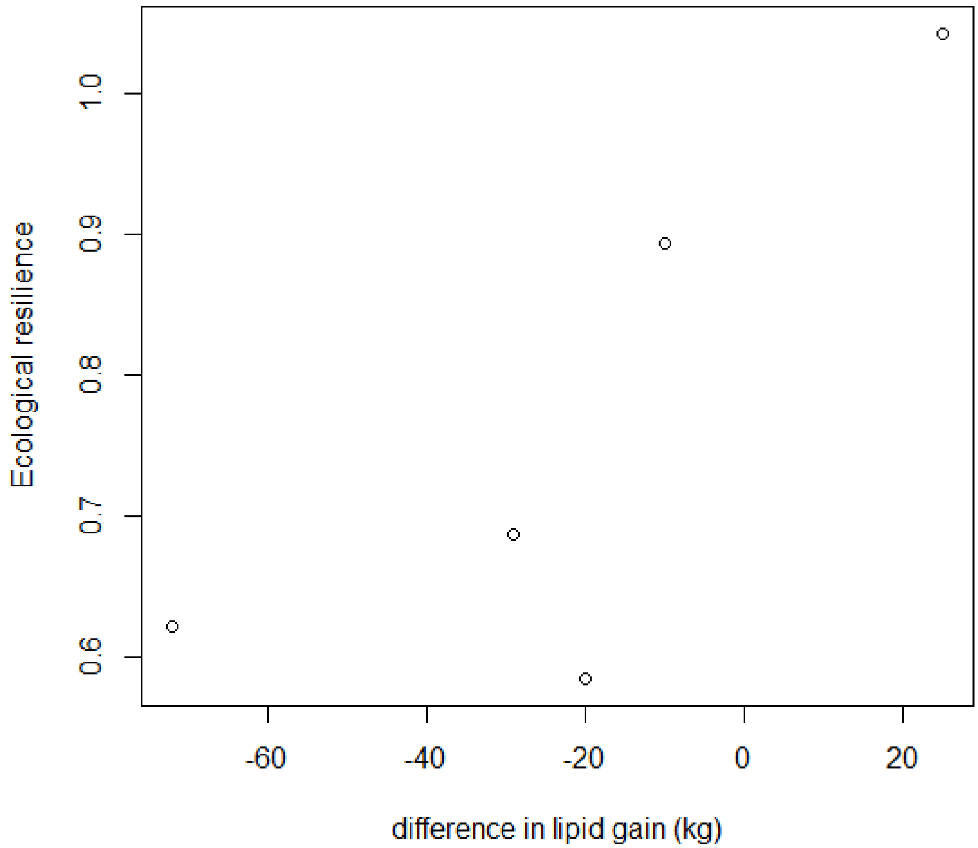

Figure 2: Reactivity of northern elephant seals predicts El Nino performance
Higher ecological resilience, or reactivity, appears to correlate with good performance in an El Nino year compared with typical climate years. Each data point represents an individual female elephant seal for which we have full foraging tracks in both an El Nino year and a typical year.

IMPACT/APPLICATIONS

[Potential future impact for science and/or systems applications]

RELATED PROJECTS

NONE

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PUBLICATIONS

S Nattrass and D Lusseau (2014) Using resilience to predict the effects of disturbance; Current Biology [submitted]

CONFERENCES

- Society of Mathematical Biology/Japanese Society of Mathematical Biology Joint Annual Meeting. Osaka, Japan, July 28 – August 1 2014. Twenty minute oral presentation on all aspects of the project.
- Animal Behavior Society Annual Meeting. Princeton, NJ, USA, August 9-13 2014. Twelve minute oral presentation on fitting developed resilience measures to data from northern elephant seals.
- Models in Population Dynamics and Ecology. Turin, Italy, August 25-29 2014. Twenty minute oral presentation on all aspects of the project.